

**Survival and Growth of Seedlings
of Scots Pine Provenances
at Varying Nutrient Levels**

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JAMES H. BROWN¹

INTRODUCTION

Scots pine (*Pinus sylvestris* L.) is one of the most widely distributed tree species in the world. Within its natural range it shows wide variation which has been the subject of a number of provenance studies emphasizing such traits as growth rate, stem form, needle length and color, winter injury, etc. (13, 14, 15). A few studies have shown distinct differences between Scots pine provenances in root systems (2) and in reaction to cultural treatments (1, 3).

Many differences between Scots pine provenances have been related to environmental conditions, particularly temperature and moisture, in the area of origin. Provenances also evolved under widely diverse soil conditions and it is probable that nutrient requirements vary accordingly. Investigations with Scots pine have shown that different provenances grown on the same site or under uniform greenhouse conditions varied significantly in their uptake and foliar concentrations of various elements (5, 11, 12).

Ingestad (6, 7, 8, 9) has shown that seedlings of Scots pine, *Picea abies*, and *Betula verrucosa* grow best in a root medium containing different total nutrient concentrations but the same ratio of one element to another (Table 1). Maximum shoot growth of seedlings usually occurred at nutrient concentrations above those for best root growth. Best quality Scots pine seedlings having sufficient top growth and good top-root balance were produced when nitrogen in the root medium was maintained at 50 ppm, with a total elemental concentration of 101.45 ppm and pH about 4.9 (Table 3).

In an earlier exploratory study (4), seedlings of Scots pine provenances from Spain, Germany, and Sweden were grown from seed in the greenhouse using an inert potting mixture to which three levels of a complete (20-10-20) fertilizer had been added. There were significant differences, with seedlings of the Spanish origin growing better at lower nutrient levels than the German and Swedish trees. Detection of small differences between seedlots or determination of "optimum" nutrition levels for best growth was not possible.

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Purposes of studies reported here were: 1) to investigate variations in survival and growth of seedlings of a larger number of Scots pine provenances grown at a wider range of nutrient levels, and 2) to determine concentrations of a balanced nutrient solution desirable for optimum growth of seedlings of different Scots pine seed sources.

METHODS AND MATERIALS

Two separate studies were conducted. In the first, seedlings of 10 provenances of Scots pine were grown at 5 nutrient levels for 8 months.

TABLE 1.—Proportions of Elements in Root Media for Optimum Growth of Scots Pine Seedlings (9).

Element	Proportion, Percent by Weight
Nitrogen	100
Phosphorus	13
Potassium	65
Calcium	6
Magnesium	8.5
Sulfur	9
Iron	0.7
Manganese	0.4
Boron	0.2
Copper	0.03
Zinc	0.03
Molybdenum	0.007
Sodium	0.003
Chlorine	0.03

TABLE 2.—Locations and Soils of Area of Seed Collections for Scots Pine Provenances Used in Studies of Variations in Nutrient Requirements.

Country of Origin	Latitude °N	Longitude °E	Elevation m	Soil and/or Parent Material
Sweden	57.6	15.6	100	Gravel moraine
Scotland	57.2	— 3.7	250	Thin peat over glacial moraine
North-France	49.0	7.5	250	Siliceous from Vosges sandstone
Czechoslovakia	48.9	16.2	425	Serpentine
South-France	45.3	3.7	1000	Granite
Yugoslavia	44.9	15.4	725	Podzol
North-Spain	42.6	— 0.4	1300	Siliceous derived from granite
Greece	41.2	23.5	1400	Gneiss and granite
Central-Spain	40.8	—3.3	1500	Gneiss and granite
Turkey	40.0	31.1	1450	Calcareous

Based on results from that study, 6 provenances were chosen (2 each exhibiting relatively low, intermediate, and high nutrient requirements in Study 1) and seedlings were grown at 11 nutrient levels for 6 months.

Provenances

Seeds of Scots pine were obtained from research cooperators in Europe. Each seedlot was collected from 10 or more average trees in a stand of several acres. Detailed origin data and limited soils and/or soil parent material data were provided for each seed source (Table 2).

Nutrient Solutions

Seedlings were grown in a series of nutrient solutions, all of which contained the same ratio of one element to another determined by Ingestad (9) to be best for growth of Scots pine (Table 1). The control level was set at the concentration determined by Ingestad to be "optimum" for growth of Scots pine of an undesignated seed source and intervals between levels were chosen to provide a range from deficiency to near toxic high levels for individual seedlings and/or provenances (Table 3).

Cultural Techniques

Seedlings were grown using an aerated solution culture. Plastic pots were filled with 3.5 liters of fine (3 - 6 mm), inert silica gravel. To each pot, 1.5 liters of nutrient solution was added (sufficient to keep solution at or near surface of gravel). A manifold system attached to a compressed air source provided continuous aeration.

TABLE 3.—Concentrations of Nutrient Solutions Used in Studies of Variation in Nutrient Requirements of Scots Pine Provenances.

Study 1	Study 2	Total Elemental Concentration	Percent of Control Concentration*
		ppm	
1	1	10.145	10
	2	40.580	40
2		55.800	55
	3	71.015	70
3*	4*	101.450*	100*
	5	152.175	150
	6	202.900	200
	7	304.350	300
	8	405.800	400
4		557.975	550
	9	608.700	600
	10	811.600	800
5	11	1014.500	1000

*Control concentration based on optimum for growth of Scots pine (of undesignated provenance) as determined by Ingestad (9).

Seed was germinated in inert silica sand; 1 week after germination, two seedlings per seedlot were transplanted into each pot, with three pots (replicates) per seedlot. All pots were filled initially with nutrient solution at the lowest concentration (Table 3). After 1 week, pots were drained and refilled with nutrient solutions at levels used in the respective studies, 5 in Study 1 and 11 in Study 2. Thereafter, nutrient solutions were changed weekly throughout the 8- and 6-month lengths of Studies 1 and 2, respectively. Supplemental incandescent and fluorescent lighting maintained a minimum 16-hour light period. Light intensity during the light period varied from approximately 700 to 6,000 foot candles, depending on time of day and/or year. At the end of each experiment, seedlings were removed from pots and washed. Each was cut into top and root, measured, and weighed on an oven-dry basis.

Statistical Analyses

A plot was the one or two seedlings surviving in a pot and plot means were used as items in analyses. The experiments were analyzed as completely randomized factorials, with 10 provenances, 5 nutrient levels, and 3 replications in Study 1 and 6 provenances, 11 nutrient levels, and 3 replications in Study 2. In addition, separate single factor analyses of variance were run for individual provenances and/or nutrient levels to permit statistical comparison of differences which might be obscured by large variations in survival and growth at the wide range of nutrient levels.

RESULTS AND DISCUSSION

In both studies, there were statistically significant differences (0.01-0.05 probability levels) due to provenance, fertility level, and interactions between the two for all plant parts studied. In view of objectives of the studies, only main effects for provenance and provenance x fertility level interactions will be discussed.

Survival

In Studies 1 and 2, all seedlings survived at nutrient concentrations up to and generally well above those reported by Ingestad as optimum for growth of Scots pine seedlings (Table 4). There were significant differences between provenances in survival of seedlings at nutrient concentrations 550 and 1,000 percent of the control in Study 1 and 600 to 1,000 percent of the control in Study 2. In Study 1, best average survival for the two highest nutrient concentrations occurred for seedlings of Scottish, south-French, and Turkish origins; in Study 2 it was best for seedlings of south-French and Turkish provenances and survival of seedlings of those origins was also best at individual nutrient levels 6, 8, and 10 times that of the control.

Poorest average survival at the two highest nutrient levels in Study 1 occurred for seedlings of provenances from northern France, Yugoslavia, northern and central Spain, and Greece. In Study 2, average survival at higher nutrient concentrations was lowest for seedlings of seed sources from Yugoslavia and central Spain and survival of seedlings of those origins was also lowest at all individual levels 4 to 10 times that of the control solution (Table 4).

For seedlings of provenances from Sweden and Czechoslovakia, average survival values and survival at individual higher nutrient levels were generally intermediate and statistical significance usually overlapped that for the two groups discussed previously in both studies.

Seedling Growth

Total weights of seedling tops and roots were most indicative of changes in nutrient concentrations and are used as the primary basis for comparisons that follow. Stem and needle weights showed similar response to changes in nutrient levels and in most cases maximums for the two occurred at the same concentration; where they did not, variation was never more than one nutrient level above or below that for total top weight. Lateral root weights also closely paralleled total root weights and in nearly all instances, maximums for the two were at the same nutrient level. Highest tap root weights always occurred at a

TABLE 4.—Percent Survival of Seedlings of Scots Pine Provenances Grown in Balanced Nutrient Solutions Having Varying Total Concentrations.*

Country of Origin	Nutrient Concentration, Percent of Control Level							
	Study 1			Study 2				
	550	1000	Av.†	400	600	800	1000	Av.†
Sweden	100	33	67	100	83	67	33	71
Scotland	100	67	83					
North-France	50	17	33					
Czechoslovakia	83	50	67	100	83	50	33	67
South-France	100	67	83	100	100	83	67	88
Yugoslavia	50	17	33	83	50	33	17	46
North-Spain	50	0	25					
Greece	67	17	42					
Central-Spain	67	17	42	83	67	33	0	46
Turkey	100	67	83	100	100	83	50	83
LSD ₀₅	31	41	25	NS	36	47	42	18

*Survival was 100% for seedlings grown at nutrient concentrations lower than those indicated.

†Average survival of seedlings grown at two highest nutrient concentrations in Study 1 and four highest concentrations in Study 2.

higher nutrient level than those at which heaviest total and lateral roots were found.

Average Weights of Tops and Roots: In Study 1, weights of seedlings of the northeastern French provenance were significantly heaviest, followed by the seed sources from Czechoslovakia and Yugoslavia. In Study 2, seedlings of origins from Czechoslovakia and Yugoslavia were first and second (Table 5). Other studies of greenhouse, nursery, and field-grown trees have identified central European origins as fastest growing of the Scots pine varieties, and rankings, based primarily on height, were similar to those in this study (2, 10, 13, 14, 15). In both studies, seedlings of the Swedish provenance had lowest top and root weights, followed by seedlings of provenances from isolated portions of the species range: northern Spain, southern France, Greece, central Spain, Turkey, and Scotland in Study 1 and southern France, central Spain, and Turkey in Study 2. Similar results, although not necessarily in the same ranking order, have been noted in other studies.

TABLE 5.—Average Weights of Tops and Roots (for All Nutrient Concentrations) for Greenhouse-grown Seedlings of Scots Pine Provenances.*

Provenance	Total Top Weight	Total Root Weight	Total Plant Weight
grams			
Study 1 (8 months)			
Sweden	4.9	1.2	6.1
Scotland	7.8	1.8	9.6
North-France	11.6	2.8	14.4
Czechoslovakia	9.1	2.3	12.4
South-France	5.9	1.4	7.3
Yugoslavia	8.7	2.2	10.9
North-Spain	5.0	1.3	6.3
Greece	6.4	1.5	7.9
Central-Spain	7.4	1.8	9.2
Turkey	7.5	1.9	9.4
LSD .05	1.0	0.4	1.2
Study 2 (6 months)			
Sweden	3.8	0.9	4.7
Czechoslovakia	7.4	1.5	8.9
South-France	5.0	0.9	5.9
Yugoslavia	7.1	1.5	8.6
Central-Spain	5.3	1.3	6.6
Turkey	6.2	1.4	7.6
LSD .05	0.6	0.2	0.7

*Average weights based on seedlings that survived at all nutrient levels

Provenance-Fertility Interactions for Heaviest Top Weights:

In both studies, there were significant differences between provenances in nutrient levels at which highest seedling shoot weights occurred (Tables 6 and 7). In Study 1, seedlings of origins from Scotland, Czechoslovakia, and Turkey had heaviest tops at the nutrient level 5.5 times that of the control solution, while shoots of the seed source from northern Spain were heaviest at the control level. Seedlings of the remaining six provenances had statistically similar highest shoot weights at nutrient levels 1 and 5.5 times that of the control. Of those six, however, only the Swedish origin had 100% survival at the concentration 5.5 times that of the control (Table 4).

Results in Study 2 were better defined. Seedlings of the south-French and Turkish provenances required the highest nutrient levels for maximum shoot weights (1.5 to 3.0 times that of the control), while seedlings of seed sources from central Spain and Yugoslavia had lowest nutrient requirements for heaviest top weights (1.5 times the control). Shoots of seedlings of provenances from Sweden and Czechoslovakia were heaviest at concentrations 1.5 to 2.0 times the control.

Provenance-Fertility Interactions for Heaviest Root Weights:

Root weights were more sensitive to changes in nutrient concentrations than were top weights. In both studies, root weights usually reached maximums at well-defined peaks and weights were significantly lower above and below those maximums (Tables 6 and 7). Additionally, the tap root became an increasingly larger component of the root system at nutrient levels above those where highest total root weights occurred. In Study 1, total root weights were heaviest for seedlings of all provenances at the control concentration (Table 6). In Study 2, root weights generally paralleled top weights, except that maximums were reached at one to three nutrient levels below those where heaviest tops were produced.

Ingestad (6, 7, 8) noted similar results. Highest seedling root weights occurred at nutrient levels: 100 to 200% of the control for the Turkish source; 100 to 150% of the control for those of the Swedish and south-French origins; at the 100% level for those of the Czechoslovakian provenance; and 70 to 100% of the control for seedlings of origins from Yugoslavia and central Spain.

Relative Weights of Tops and Roots at Low and High Nutrient Levels: As indicated in Tables 6 and 7, weights of seedling tops and roots increased rapidly in response to increasing nutrient concentrations at lower nutrient levels and once maximums were reached, weights declined gradually in response to further increases in nutrient concentration. Similar results were noted by Ingestad (6, 7, 8). In both of the

TABLE 6.—Relative Weights of 8-Month-Old Seedlings of Scots Pine Provenances Grown at Varying Nutrient Levels in Study 1.*

Nutrient Level Percent of Control	Provenance										LSD ₀₅
	SWE	SCOT	N-FRA	CZECH	S-FRA	YUGO	N-SPA	GRE	C-SPA	TURK	
	Percent of Seedlot Mean										
Total Seedling Top											
10	1	2	2	1	1	3	5	3	4	2	1
55	60	58	74	60	54	75	92	86	78	57	15
100	173	175	145	141	161	147	161	136	156	147	16
550	162	208	149	162	166	147	141	138	148	168	25
1000	104	80	126	136	119	123		117	114	126	†
LSD ₀₅	20	21	19	20	24	21	19	20	16	20	
Total Seedling Root											
10	7	8	11	6	6	16	24	16	21	8	5
55	100	95	124	116	93	121	127	123	125	97	21
100	190	186	151	186	218	171	164	155	176	192	26
550	133	165	120	137	127	131	88	112	113	124	28
1000	69	60	94	102	71	72		96	66	81	†
LSD ₀₅	17	21	25	23	19	22	22	22	24	26	

*Relative weights based on seedlot means listed in Table 5.

†Insufficient data for statistical analyses because of high mortality of seedlings (Table 4).

present studies there were significant differences between provenances in relative weights (values expressed as a percent of provenance means) of seedlings at individual nutrient levels, particularly at lower concentrations (Tables 6 and 7). In Study 1, significantly higher relative weights at nutrient levels below the control occurred for seedlings of provenances from northern Spain, Greece, central Spain, northern France, and Yugoslavia; in Study 2, they were highest for seedlings of origins from central Spain and Yugoslavia. Relative weights at lower nutrient levels were generally lowest for seedlings of Scottish, south-

TABLE 7.—Relative Weights of 6-Month-Old Seedlings of Scots Pine Provenances Grown at Varying Nutrient Levels in Study 2.*

Nutrient Level Percent of Control	Provenance						LSD ₀₅
	SWE	CZECH	S-FRA	YUGO	C-SPA	TURK	
	Percent of Seedlot Mean						
Total Seedling Top							
10	2	1	1	3	3	1	1
40	34	31	24	36	40	22	13
70	58	59	49	70	75	49	17
100	150	104	123	100	101	93	30
150	178	168	160	172	172	156	NS
200	174	163	158	158	150	165	NS
300	134	140	152	146	138	160	NS
400	121	129	126	134	122	139	NS
600	106	124	120	120	109	129	NS
800	81	99	105	92	98	96	†
1000	64	82	80	71	88	72	†
LSD ₀₅	20	21	21	21	21	20	
Total Seedling Root							
10	7	7	7	16	18	7	5
40	69	79	54	104	96	51	23
70	99	116	78	165	151	85	27
100	189	171	158	163	156	161	NS
150	186	158	158	123	127	167	31
200	162	132	154	114	118	162	30
300	117	122	127	113	115	134	NS
400	98	110	106	103	101	115	NS
600	71	84	98	85	87	94	NS
800	51	61	76	72	69	71	†
1000	38	29	68	46	59	51	†
LSD ₀₅	24	25	23	28	27	27	

*Relative weights based on seedlot means listed in Table 5

NS—Differences not statistically significant.

†Insufficient data for statistical analyses because of high mortality of seedlings (Table 4).

French, and Turkish provenances and intermediate for seedlings of Swedish and Czechoslovakian origins.

Differences in relative weights of tops and roots at nutrient concentrations above the control level were not as well-defined. Seedlings of provenances which had best relative growth at levels below the control had lowest relative weights of tops and roots at 5.5 times the control level in Study 1 and roots had lower relative weights at levels 1.5 and 2.0 times the control in Study 2. However, there were no consistent differences between groups which had shown low to intermediate relative weights at levels below the control concentration (Tables 6 and 7).

Seedling Shoot and Needle Lengths, Averages and Nutrient Levels for Maximum Growth: Differences between provenances in average top lengths followed trends for seedling weights discussed pre-

TABLE 8.—Average Top and Needle Lengths and Nutrient Concentrations at Which Maximum Lengths Occurred for Greenhouse-grown Seedlings of Scots Pine Provenances.

Provenance	Average Length		Nutrient Levels for Maximum Length*	
	Top	Needles	Top	Needles
	mm		Percent of Control Level	
Study 1 (8 months)				
Sweden	156	101	100-550	100-550
Scotland	194	101	100-550	55-550
North-France	238	141	100-550	55-1000
Czechoslovakia	216	137	100-550	100-1000
South-France	159	90	100-550	100-1000
Yugoslavia	207	110	100-550	55-550
North Spain	149	82	100-550	100-550
Greece	186	106	100-550	55-1000
Central-Spain	174	92	100 550	55-550
Turkey	178	116	550	55-1000
LSD .05	20	13		
Study 2 (6 months)				
Sweden	122	103	150-400	150-600
Czechoslovakia	158	140	100-300	150-400
South-France	118	98	150-300	100-1000
Yugoslavia	143	117	100-300	100-800
Central-Spain	135	95	150-300	150-800
Turkey	130	118	100-400	100-400
LSD .05	12	9		

*Nutrient levels for maximum growth as determined using Duncan's multiple range test with 0.05 probability level.

viously for these studies and also trends for top lengths shown for Scots pine in other studies (2, 13, 14, 15). Seedlings of central European provenances from northern France, Czechoslovakia, and Yugoslavia were tallest and those from Sweden, northern Spain, and southern France were shortest. However, top lengths did not show close response to variations in nutrient concentrations. In Study 1, statistically similar maximum shoot lengths for individual provenances usually occurred over a range of two nutrient concentrations, while in Study 2, maximums were found over a range of three to five levels (Table 5).

Ranking of provenance needle lengths was also approximately the same as those noted in other studies (13, 14, 15). Seedlings of seed sources from northern France and Czechoslovakia had longest needles and those from northern and central Spain and southern France had the shortest (Table 8). However, average lengths of needles were considerably longer than those noted in other studies, probably because a majority of nutrient concentrations in both studies were at levels favorable for maximum needle growth. Needle lengths generally reached maximums at or one or two nutrient levels below those at which maximum top weights were found. Above that point, needle lengths remained approximately constant up to concentrations near the highest used.

CONCLUSIONS

Seedlings of Scots pine provenances grown in these studies were characterized by certain combinations of traits, depending on their comparative nutrient requirements. Those having best growth at relatively high nutrient levels also had better survival at highest concentrations and slower relative growth at lower levels. Conversely, seedlings of origins displaying relatively low nutrient requirements had very poor survival at higher nutrient levels and faster relative growth at low nutrient concentrations. No relationships were noted between nutrient requirements of seedlings of different provenance and average weights and/or lengths of seedling shoots, roots, or needles.

Designation of optimum concentrations of the balanced nutrient solution used in these studies for growth of seedlings of different Scots pine provenances can best be based on levels at which maximum root growth occurred. At that concentration, top growth would not be at its greatest but tops would be sufficiently large to provide seedlings with excellent top-root balance. Survival at higher nutrient concentrations and relative growth at lower levels can also be used as a guide, particularly for those provenances used in Study 1 but not Study 2.

The following three groups are recognized, based on the control concentration set at Ingstad's (9) optimum (101.45 ppm total concen-

tration) for growth of Scots pine seedlings: 1) optimum total concentration 70 to 100 ppm: northern France, Yugoslavia, northern and central Spain, and Greece; 2) optimum total concentration 100 to 150 ppm: Sweden and Czechoslovakia; and 3) optimum total concentration 100 to 200 ppm: southern France, Turkey, and Scotland.

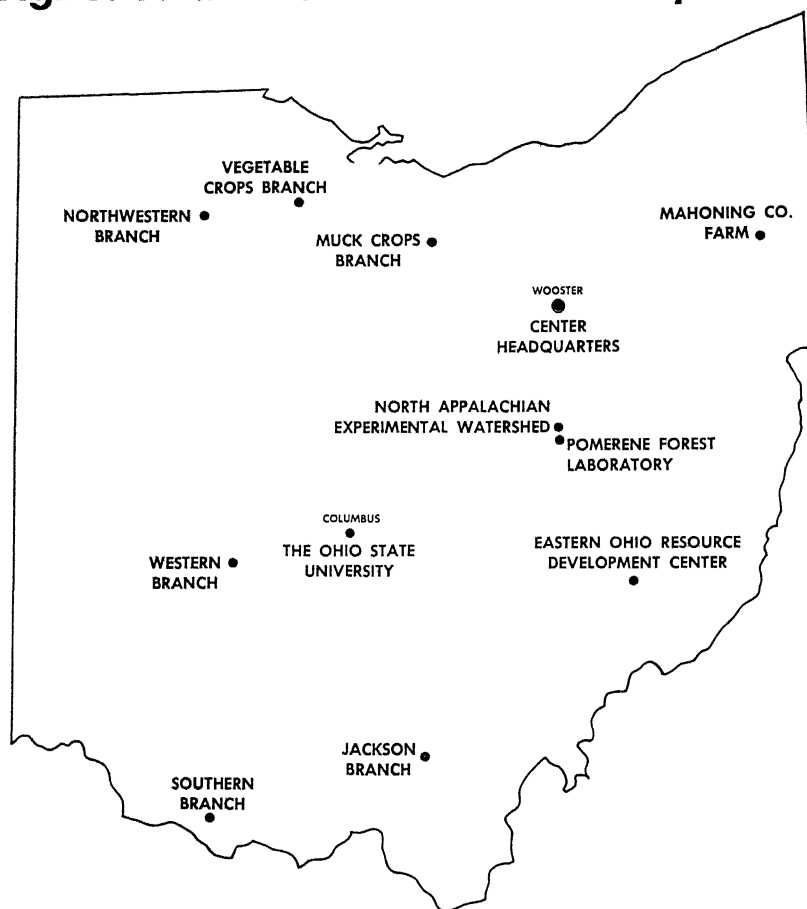
Although there were significant differences in nutrient requirements for the 10 greenhouse-grown seed sources of Scots pine used in these studies, additional research is needed to determine if those differences would be of importance under field conditions. However, there are a number of possibilities. High fertility levels maintained in many forest nurseries could result in seedlings with higher than desirable top-root balance for many commonly grown provenances of Scots pine. Also, if characteristics observed in the greenhouse carry over to out-planted seedlings, relatively rapid growth of some seed sources at lower nutrient levels could improve survival and establishment on low fertility sites. Additionally, ability to survive at higher concentrations might prove advantageous to survival and growth on sites where high salt concentrations are present in soil, such as near roadsides.

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